



Cetacean vocal learning and communication

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The cetaceans are one of the few mammalian clades capable of vocal production learning. Evidence for this comes from synchronous changes in song patterns of baleen whales and experimental work on toothed whales in captivity. While baleen whales like many vocal learners use this skill in song displays that are involved in sexual selection, toothed whales use learned signals in individual recognition and the negotiation of social relationships. Experimental studies demonstrated that dolphins can use learned signals referentially. Studies on wild dolphins demonstrated how this skill appears to be useful in their own communication system, making them an interesting subject for comparative communication studies.

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Introduction

Cetaceans have long been seen as cognitively advanced and complex in their communication [1]. This has made them a focus for comparative studies on the evolution of complex communication and human language. However, comparisons of cetacean skills with those of primates are often hampered by limited data. Cetaceans are difficult to study due to their aquatic lifestyle. Many aspects of primate cognition have not been studied in these animals. Cetaceans also have an unusual neuroanatomy which makes comparisons of brain size and encephalisation across taxa less meaningful than in other animals [2]. Nevertheless, cetaceans are capable of sophisticated vocal production learning, which stands in stark contrast to a lack of evidence for vocal learning in nonhuman primates [3]. This review will present the evidence for vocal learning in cetaceans, show how the animals use this skill in their social behaviour and draw conclusions of its relevance for comparative communication research.

Vocal learning in cetaceans

Vocal learning can affect different aspects of communication [4]. In contextual vocal learning, animals learn to associate existing signals with novel contexts. This can affect when a signal is used (usage learning) or what meaning a call carries for the receiver (comprehension learning). In vocal production learning, an animal learns to modify its signal in form as a result of experience with signals of other individuals [4]. This includes the production of novel signals or modifications of signals that were already in an animal's repertoire. Vocal learning often combines production and contextual learning by learning novel signal types and when to use them. Contextual learning is common in animals and can be demonstrated by training an individual to give signals from its repertoire in response to a conditioned stimulus. In marine mammals, this has been demonstrated for the grey seal [5] but also for bottlenose dolphins [6] and beluga whales [7].

Vocal production learning is much rarer and in mammals only occurs in cetaceans, bats, pinnipeds and elephants [3,8]. In a classic paper, Richards *et al.* [9] showed that bottlenose dolphins can imitate novel whistle patterns and use these newly learned calls to label objects. This combination of vocal production and usage learning demonstrated that dolphins are capable of referential use of learned acoustic signals, a skill only demonstrated in dolphins, parrots and humans [1]. Later work demonstrated that vocal production learning is involved in the development of bottlenose dolphin recognition signals which are also called signature whistles [10,11].

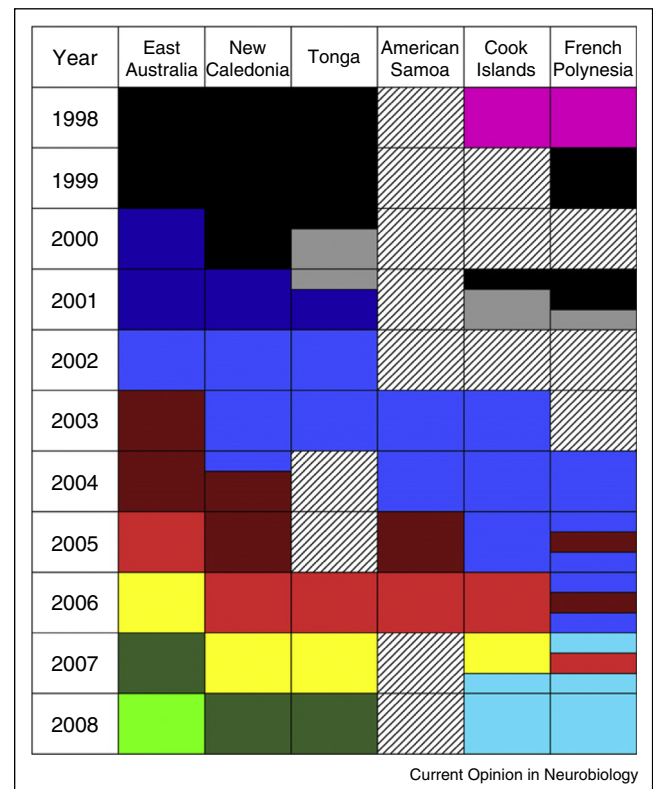
Other toothed whales show a similar propensity for vocal production learning. Anecdotal studies of belugas [12,13] and killer whales [14] reported that they can imitate signals from other species. A detailed study of a beluga whale calf showed that the animal started to produce its father's main call only after the father had been added to the group [15], hinting at a use of learning in vocal development. Analyses of the repertoires of killer whale groups in captivity and the wild also suggested that they learned novel calls from conspecifics [14,16–18]. While these are clearly remarkable vocal learning skills, few studies have tried to investigate the constraints on flexibility in vocal skills in toothed whales. Interestingly in killer whales, acoustic similarity between populations in the same ocean basin do not correlate with geographic distance [19], a pattern that could be expected for learned signals and that has been found in other species such as the bottlenose dolphin [20]. Structural similarities within killer whale call types across different matrilineal units can be influenced by social association frequencies

as would be expected for a learned signal [21]. However, different parameters of the same call types do not show the same similarity patterns across social units. Parameters can change over time in different directions [22] leading to differences in similarities depending on what parameters are analysed [23]. Shapiro *et al.* [24] suggested that killer whale calls contain additional sub-units, which may require separate analysis efforts to unravel the clearly complex patterns of dialect evolution.

Evidence for vocal learning in baleen whales is even harder to come by than in small toothed whales. The first discovery of vocal learning in this clade came from field observations that showed that all males within the Hawaiian breeding grounds sing the same song at any one time, but that the song elements in each theme changed over time [25]. Thus, whales somehow synchronised their changes, which could only be achieved through vocal learning. Such synchronous changes of song throughout a whole population have not been found in other vocal learners. Studies in the southern hemisphere have now revealed how song can change radically from one year to the next [26**]. Humpback whale song types seem to move from West to East through the southern Pacific without evidence for large shifts in ranging patterns of individual whales [27**]. Songs first recorded off Eastern Australia could be found around French Polynesia approximately 6000 km away only one year later (Figure 1). It is currently unclear why these displays drift in that way. One proposed mechanism is song transfer in high latitude foraging grounds where animals from different populations can hear each other singing [28]. Another possibility is that small numbers of animals travel with the Antarctic current in an easterly direction and introduce their song to new areas. However, why all animals in an area decide to use the novel song once it is introduced is unclear. Just as in toothed whales, genetic constraints have not received much research attention, but humpback whales do share a repertoire of social calls that are not used in songs and remain stable over time [29]. These may develop with a stronger genetic influence than song.

Other baleen whales produce sounds as well, but learning is more difficult to detect here since most of their songs consist of single song notes that do not show much variation. However, in right whale social calls [30] and in blue whale song [31] it has been found that the average frequency of these notes changed over time throughout a population. In blue whales, this frequency is matched closely between individuals within any given year, but decreases over time across years [31]. Bowhead whales show an intermediate song complexity. Their song seems to change completely from year to year but all animals sing the same song at any one time [32]. This pattern appears to be similar for what was found in southern hemisphere humpback whales, but we do not know

Figure 1



Humpback whale song types identified in the South Pacific Ocean from 1998 to 2008. Populations are listed from west to east across the region. Each color represents a distinct song type; song type colors are as follows: black, grey, pink, dark blue, blue, light blue, dark red, light red, yellow, dark green, and light green. Two colors within the same year and location indicate that both song types were present. In these cases, the seasons are broken into three periods (early, middle, and late) to indicate when a new song type was recorded. Crosshatching indicates no data available. This figure was published in [27**], Copyright Elsevier (2009).

whether song types drift geographically as in humpback whales or whether they disappear completely.

The use of learned signals in cetaceans

In toothed whales, vocal learning and other cognitive skills have often been seen as a result of complex social behaviour and the necessities of negotiating and maintaining social relationships in a large society. The usage of calls in killer whales [33] and of whistles in bottlenose dolphins [34] suggests that their main function is to maintain spatial group cohesion and to negotiate social relationships mainly because of the contexts in which they are produced. In aquatic animals, acoustic signals are particularly suited to maintain contact when animals are spatially separated since sound transmits over larger areas in water than in air. However, large acoustic ranges also lead to high noise levels caused by the signals of other animals within detection range [35]. Learning may have

evolved here to encode identity in frequency modulation patterns or to shift the frequency range used to communicate [3]. This kind of encoding reduces interference with noise. Frequency modulation patterns are also relatively resistant to deterioration with distance.

The most detailed information for the identity and cohesion function of learned signals comes from bottlenose dolphins. Bottlenose dolphins develop individually distinctive signature whistles in the first few months of their lives [36]. The development of this whistle is influenced by vocal learning in that each individual develops its own novel, unique frequency modulation pattern after listening to whistles in its environment [10]. Signature whistles function in individual recognition [37] and spatial group cohesion [38]. Animals at sea exchange signature whistles before they join other groups but do not engage in such exchanges if passing other groups, making signature whistles an important part of an approach [39^{*}]. Since the exchange leads to groups joining, it appears to be an affiliative signal in which animals exchange information on their identities. In whistle sequences, bottlenose dolphins leave a one second window between whistles in which others can respond. In captivity, callers appear to avoid overlapping each other in such interactions [40] while overlapping in the wild is not uncommon [39^{*}]. Captive studies have shown that animals remember the signature whistles of animals they spent time with for at least 20 years after the last exposure to the whistle [41^{**}].

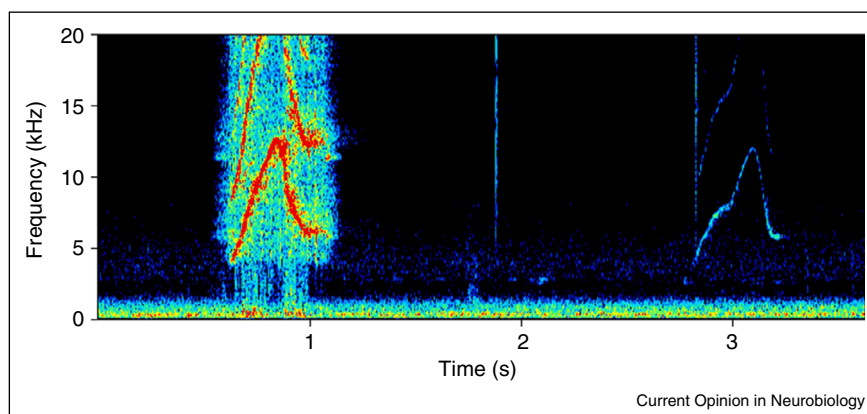
The vocal learning ability of bottlenose dolphins also allows them to copy signature whistles of conspecifics [38,42,43]. This is potentially problematic in an individual recognition system, since it makes the identity information in a whistle less reliable. However, an analysis of who copies whom and what copies sound like demonstrated that copying only occurs between closely affiliated animals

such as mothers and their calves or members of male alliances, and that copying animals introduce changes in whistle parameters while keeping the frequency modulation pattern unchanged which make copies recognisable as copies [44^{*}]. Males even use learning abilities to make their signature whistles more alike once they formed an alliance [45]. Bottlenose dolphins copy whistles primarily in affiliative interactions where no resources are at stake. This makes it different from copying interactions in most other vocal learners such as matched counter-singing in birds [46]. Copying of sounds seems to occur in other species of toothed whales as well, as demonstrated by false killer whales copying aspects of military sonar signals that they were exposed to [47] and killer whales engaging in exchanges of pulsed call types [48].

In captive experiments, it has been shown that bottlenose dolphins are capable of using novel signals to label objects [49] and that they can learn to allocate different dolphin whistles to different response paddles [50]. Given these abilities, it is intriguing to ask where this ability might be used in dolphin communication. Ever since signature whistle copying had been described [42], authors have speculated on whether such copies can function as labels for conspecifics [36]. In a recent field study, it was demonstrated that dolphins can be addressed with copies of their own signature whistles [51^{*}]. Bottlenose dolphins replied with their own signature whistle when hearing a copy of it (Figure 2), but did not show this response to other familiar or unfamiliar whistles (Figure 3). Further studies are needed to investigate whether this functions only in direct addressing, or whether animals can exchange information about third parties using these whistles.

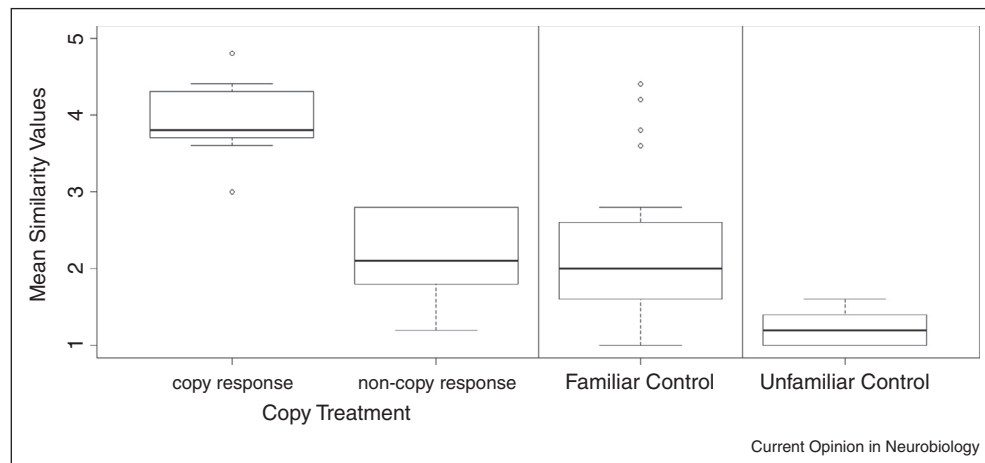
The use of learned signals in baleen whales is primarily in song. Detailed information about song interactions is only available for humpback whales. Here males sing primarily

Figure 2



Spectrogram of a bottlenose dolphin signature whistle playback and the dolphin's response. The first whistle is a playback version of the animal's signature whistle, and the second whistle is the animal's matching response. Spectrogram parameters (FFT 512, 75% overlap, Blackman window).

Figure 3



Box plots of similarity values of whistles produced in response to playback stimuli as judged by five independent, blind observers. Boxes indicate interquartile ranges, middle lines indicate medians and whiskers indicate values within 0.7 inter-quartile ranges of the lower and upper quartiles. Outliers are shown as separate dots. Similarities were rated on a 1 (low similarity) to 5 (high similarity) scale. Observers had significant agreement in their judgement (Cohen's $\kappa = 0.46$, $z = 22.5$, $P < 0.0001$). A similarity of 3 or higher was considered to be a copy response. Sample sizes were 12 playbacks for copy treatments (8 with a copy response and 4 with a non-copy response), 12 playbacks for familiar controls and 10 playbacks for unfamiliar control playbacks. Note that outliers in the familiar controls come from two playbacks and may have resembled signature whistles of other animals in the population. This figure was published in [51], Copyright National Academy of Sciences (2013).

during the breeding season. Migrating males tend to start singing once they have joined a female and tend to sing longer when with females suggesting its function in mate attraction and selection [52]. However, singing males also show aggression towards other singers [53] and are generally spaced further apart than non-singing males [54], suggesting that it also has a function in intra-sexual selection. While the singing pattern with a shared song that changes almost continuously across an entire population is unusual in singing animals, most data on the functional use of song is very similar to what we find in birds. Thus, song learning appears to be linked to sexual selection [55], most likely facilitating fitness assessments within and between the sexes.

Cetaceans changing signals in response to anthropogenic noise is not uncommon and suggests that vocal learning can help animals to cope with noise pollution [56,57]. Strategies here include changing timing of calls [34], shifting frequency bands [58], increasing duration [22] or amplitude [59] as in the Lombard effect or increasing the redundancy in signal displays [60]. Not all of these necessarily involve vocal learning, but they appear to be effective means of improving signal transmission. As discussed above, noise may have contributed to the evolution of vocal learning in cetaceans, which may help them to adjust to anthropogenic noise.

Conclusions

Cetaceans are a clade that is far removed from the primates and are therefore of little relevance to the direct

evolution of human language. However, it is remarkable that they share many cognitive skills with primates. In delphinids, we find social structures of similar complexity as in primates and a use of learned vocalizations in social interactions that is absent in nonhuman primates. Evidence for the comprehension [61] and use of pointing gestures [62], an understanding of syntactical structure in artificial communication systems and the ability to use learned signals referentially [49], make us wonder what evolutionary forces could have led to such similarities with primates when the environments in which these skills evolved in the two groups could not have been more different. The most parsimonious answer is that complexities in social relationships and systems are the main driving force for the evolution of complexity in communication and cognition across taxa. The reliance on acoustic signals in the marine environment could have accelerated the evolution of acoustic skills and established vocal learning skills in dolphins while primates could rely on already existing learning abilities in movement patterns to introduce complexity to their communication in the gestural domain. Thus, the evolution of vocal learning in humans would have been driven by the need to maintain this complex communication when visual contact was not possible. While toothed whales do not appear to use song, singing is common in baleen whales where social structures are less complex. Thus, vocal learning in cetaceans may have evolved in a sexual selection context and was then later available for use in social negotiations when more complex social systems evolved in the toothed whales. Alternatively, it could have evolved in the context

of individual recognition primarily between mothers and calves, a context in which all cetaceans use elaborate contact calls. Comparisons between primates and cetaceans are a fruitful approach to understanding what traits may be unique in the evolution of human language or how similar traits could have evolved in such different environments. This will allow us to hypothesize on the origins of complexity in communication systems and produce accurate comparisons of human and animal communication.

Conflicts of Interest

Nothing declared.

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